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EVOLUTION IN MICROSCOPIC PLANTS[1]

By CHARLES EDWIN BESSEY

Although there are many students of the lower forms of plants and although many microscopists give much time to the examination of the simpler algae and fungi, they are too generally studied as *mere forms,* little or no attention being given to their relationship to one another, or to questions as to their origin and development. We have heated discussions as to little details of structure,—as in the case of the markings on the diatom wall,—while we have nothing in regard to the meaning and origin of these markings and other details. Perhaps this is a result of the excessive appreciation of facts which modern laboratory science has given us. We have come to such a pass that often the only things we appreciate in an investigation are the structural facts brought out, while we overlook as unworthy of our serious attention the deeper meaning and significance which are equally obvious. How rarely do we find that a student of the bacteria, the fresh-water algae, the fungi, the lichens, the liverworts, mosses, or ferns, sees in the varied and beautiful forms the thread of evolution which binds them all together. And yet it is true that these lower forms of plants show the method of evolution more clearly than do the higher plants. These simple organisms are more plastic, they respond more readily to their environment, than do the higher forms, which have become more stabilized. Here I might speak of experimental results, but these must be passed by now for want of time. In this address I can only glance at some of the more marked indications of evolution, as brought out in their natural classification.

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[1] Condensed from the notes of an oral address.

Away down at the beginning of the vegetable kingdom are the minute single-celled protophytes or water-slimes (*Chroococcus, Gloeocapsa,* etc.) in which each plant consists of a bit of faintly colored protoplasm surrounded by a thin wall. There is no definite nucleus here, and the only indications of nuclear matter are a few granules scattered in the protoplasm. We can scarcely conceive of simpler living things. Near them and a little higher are the blue-green water-slimes (of the families Oscillatoriaceae, Nostocaceae, Scytonemaceae and Rivulariaceae) in which the cells cohere in elongated filaments. In the lowest of these the cells are quite undifferentiated, all the cells of a filament being apparently exactly alike, but in the subsequent families some differences appear. Thus in the nostocs there are here and there larger cells (heterocysts) among the otherwise similar cells. In the rivularias the differentiation is carried a step further, the cells gradually diminishing in diameter from one end to the other. In all these plants the individual cells are yet very simple. The walls are a little more defined in the higher forms, and the nuclear matter, while still consisting of separate granules, is a little more condensed.

In the lower green-slimes (Protococcaceae) we find at once evidence of marked improvement. The most significant advance is in the development of a distinct nucleus. Instead of a collection of granules lying in the protoplasm we have here a rounded body sharply set off from the surrounding cytoplasm. Here, also, the coloring matter of the cell is no longer diffused throughout its protoplasm, but it is restricted to one or more protoplasmic masses (chromatophores) which lie in the colorless cytoplasm.

But the greatest advance is made in the methods of reproduction. While in the protophytes new plants are formed only by the fission of the cells, in these green-slimes we find for the first time that cells may divide into several motile zoospores. These may swim about for a time, and then come to rest, when they form walls, and are quite like the cells from which they sprang. This motility is clearly a device for the distribution of the plants, and in fact each zoospore is to be regarded as a young plant which is able to move away from the plants in whose midst it originated, and thereby to live in a less crowded environment. Some of these zoospores, however, do not settle down in the manner described, but two meeting, fuse into one cell, which is consequently larger and stronger, and more capable of enduring adverse conditions than either of the cells which enter into its composition. In this simple fusion of zoospores we have the beginning of that series of mechanisms which gradually increases in complexity up to such wonderful structures as the flowers of the lilies, orchids, roses, and thistles. What a distance from this primitive sexual mechanism to that of the higher plants; and yet between these widely separated extremes there is such an easy gradation that it is not difficult for us to trace the path by which the most complex flower was evolved from this simple beginning.

The brook-silks and water-flannels (Confervoideae) show again how from the single-celled condition plants pass easily to the filamentous structure. We have here a repetition of the evolution of the filamentous plant body from the single cell which we have already noticed in the protophytes. Here, however, the filaments are composed of cells which are considerably differentiated. While in the lower brook-silks the cells as a rule are both vegetative and reproductive, in the higher forms there is a pretty sharp distinction between the cells having these two functions, and with this development we observe the setting aside of some cells whose function is neither vegetative nor reproductive, but merely mechanical, as in the "holdfast cells" of many species.

In many Confervoideae the sexual mechanism closely resembles that of the green-slimes, consisting of two equal, free-swimming zoospores, which fuse into a single cell which ultimately develops into a new plant. In other species the two fusing zoospores (now called gametes) are differentiated into two sizes, both still ciliated and motile, while in still others the larger gamete is non-ciliated and motionless, and the smaller is ciliated and very active. In fact the activity of the smaller gamete (now called the male gamete) appears to be increased directly as the female gamete becomes less active, and when the latter ceases activity altogether the former becomes extremely active. This change in the activity of the gametes involves the permanent inclusion of the female gamete in the cell in which it originates, thus affording it some protection before and after its union with the male gamete. Here is the beginning of a series of protective devices which show a gradually increasing complexity, and so admirably illustrate the principle of increasing parental care as a factor in evolution. Compare, for a moment, the zygote of *Protococcus* or *Conferva,* with no parental protection whatever, with that of *Oedogonium,* in which the wall of the parent cell affords some protection, and then contrast these with the amount of protection afforded by the parent flowering plant, in the thistle, for example, where coat upon coat of thick-walled cells surround the zygote and later the embryo plant.

In the brook-silks we have further illustrations of the modification of the plant body through the influence of a particular environment, whereby from these the group of the pond-scums (Conjugatae) has arisen. Through living in quiet waters some brook-silks became sluggish in habit. They no longer produce zoospores, since simple fragmentation of the filaments answers every purpose of zoospores, and to this sluggishness we may also ascribe the peculiarities of the conjugative sexual act of the pond-scums. From the filaments of the pond-scums it is a short step to the desmids, most of whose filaments break up still more easily than do those of the pond-scums. This easy fragmentation of the filament results in the unicellular condition of most desmids. By a similar easy fragmentation of the filament the diatoms have been evolved from the pond-scums, and here the deposition of silica in the cell wall makes necessary some peculiar structural changes, of much complexity, but of minor morphological importance. Desmids and diatoms are pond-scums in which the filaments suffer easy solution.

In like manner we may find the origin of the green-felts and their allies (Siphoneae) from the water-flannels (Cladophoraceae), by a continuation of the modification which has taken place in passing from the brook-silks (Confervaceae) to the water-flannels. While in the brook-silks the filaments are composed of cells separated by partitions, in the water-flannels the cell-like segments of the filaments are coenocytes in which there are no partitions between the component cells. In the green-felts this lack of partitions is carried one step further, and as a consequence the filaments are tubular, with partitions at long intervals only. In this way, we may assume, there arose the group of plants constituting the order Siphoneae, all of whose members are characterized by tubular, and little-septated, filaments. Even in those species in which the filaments are compacted into somewhat massive plants, this tubular character prevails.

It is instructive to glance at the chlorophyll-less members of the class of the green-algae (Chlorophyceae) which we have been considering. The more important of these are in the families of the water-moulds (Saprolegniaceae), downy-mildews (Peronosporaceae), and black-moulds (Mucoraceae). The first of these show comparatively little modification in the structure of the plant body from that of a green-felt, like *Vaucheria*. The differences are those which are related directly to the parasitic or saprophytic habits of the water-moulds. Thus, of course, there has been a disappearance of the chlorophyll, and a reduction in the size of the plant body, both of which modifications are such as we should expect under the circumstances. With these we find, also, the production of numberless, minute zoospores, which may be contrasted with the single, large zoospore of *Vaucheria;* yet here again, this is quite what we should look for in plants which through parasitism or saprophytism have become dependent upon a particular host or substratum. The great number of zoospores is directly correlated with the dependent habit of the plants.

The downy-mildews, which are mainly aerial (that is, non-aquatic), and parasitic in the tissues of higher plants, show first of all those modifications which are due to change of habitat. The aquatic adaptations are here replaced by aerial adaptations, as seen in the firmer walls, the substitution, temporarily or permanently, of conidia for zoospores, and the entire suppression of antherozoids. When these structural changes are thus accounted for, there remain few others. In fact the downy-mildews, although parasitic, have retained so many of the characteristics of the green-felts that their relationship is most evident. We may regard the downy-mildews as green-felts which have become parasitic on higher plants, and which for this reason have become modified as here indicated.

The black-moulds (Mucoraceae) have often been regarded as related more closely to the pond-scums (Conjugatae), but I am convinced that they are not so related, but on the contrary that their origin is to be sought in the green-felts, with which they are evidently related in the structure of the plant body at least. As the black-moulds are mostly saprophytic, and aerial, their reproductive apparatus is correspondingly modified. Thus there is a complete suppression of zoospores, which is effected by the simple device of the walling in of every little cell (zoospore) resulting from the division of the terminal segment (sporangium) of one of the branches. The zoosporangium has easily been modified into a sporangium containing walled spores. The spores are the homologues of the zoospores, and doubtless were derived from them. In the sexual apparatus the greatest modifications have taken place. The gametangia, instead of being quite unlike in size and shape, as they are in the green-felts, water-moulds, and downy-mildews, have suffered such degenerative modification that they are little unlike. This is, perhaps, to be correlated with their saprophytic habit, and there is little doubt that these sexual organs are on the way to extinction. The infrequency of their occurrence in the ordinary species shows that they are obsolescent, to say the least.

In passing, I may say that the group of the brown seaweeds (Phaeophyceae), although related to the green-algae, constitute a side line ending abruptly with the rockweeds and the kelps, and that no higher forms have sprung from them. No higher forms can be traced back to the brown-algae. Their evolutionary line ends with their own higher members.

Coming back to the line of the green-algae, we find at the highest point the interesting plants which constitute the genus *Oedogonium.* Here we have the highest development yet reached, especially in the reproductive apparatus; yet this is easily seen to be based directly upon the structure characteristic of other green algae. From *Protococcus,* with its free-swimming isogametes, to *Conferva, Sphaeroplea,* and *Oedogonium* there is an easy gradation by which from the first very simple sexual act there has evolved the much higher act as seen in the last genus. In *Oedogonium* the gametes are quite unequal in size, and the minute antherozoid is highly motile, while the large egg is entirely wanting in motility, and remains within the wall of the egg-cell. After fertilization the egg becomes a thick-walled zygote, protected somewhat by the surrounding wall of the egg-cell. There is to be observed here some care of its offspring by the parent plant, inasmuch as the egg is at no time without protection of the wall of the egg-cell.

This parental care is notably increased in the closely related plants of the genus *Coleochaete,* in which, after a fertilization in all essentials like that in *Oedogonium,* the parent plant covers the egg-cell, and with it the egg, with a layer of protective cells, thus constituting a primitive kind of fruit. Essentially the same structures occur in the red seaweeds, in which the parental care of the results of fertilization is often considerably more marked. Fertilization is no longer confined to the egg alone, but its stimulation extends to cells and tissues which are not at all sexual in nature, but accessory, rather, and belonging not to the new structure but to the structure of the parent plant.

Passing to the liverworts and mosses we note that the protective tissue, which in the cases cited grows around the egg-cell only after fertilization, now is developed by the parent plant long before fertilization. Yet this notable modification was anticipated in the stoneworts (Characeae), the highest of the green-algae, where the egg as it develops becomes surrounded by a protective envelope in every essential like that which surrounds the fertilized egg of *Coleochaete.*

From the liverworts to the lower ferns is but a short step, as is shown in the essential identity of the sexual organs. The egg-cell is surrounded before fertilization by a layer of protective tissue exactly as in the liverworts, and so evident is the identity of structure that egg and protective tissue have long been given the same technical name,—the " archegone." In the higher fernworts its sole modification is that it is sunken for nearly its whole length into the tissues of the parent, thus affording still greater protection to the egg before and after fertilization.

Had I the time I might speak of the gradual evolution of the plant body from the liverworts to the ferns, and flowering plants, in which step by step simpler structures are modified into those with greater and greater complexity. I can only say in passing that from one end of the series to the other there is a close continuity, and that the complex structures of the thistle and sunflower are easily derivable from the simple plant body characteristic of the lower liverworts.

The vegetable kingdom is a unit as to origin, and its multitudes of forms are connected by an unbroken series of evolutions of structure into structure. To the discerning mind there are no exceptions, no forms which are not related to others earlier than they. This evolution has not been confined to a single line, but has given rise to a multitude of branches and branchlets of the genealogical tree which represents the vegetable kingdom. Yet from the lowest there is a continuous series to each ultimate form, whatever its position, just as there is from the lowest to the highest. Evolution has been in many directions, and while the general trend has been upward, it has often been outward, and even downward, resulting in divergence, or even degeneration.